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Virtual Special Issue

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Scaling Root Processes: Global Impacts

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Virtual Issue Articles:

Cover Image: despite the importance of plant roots to ecosystem function, their inherent processes are poorly represented in mechanistic and climate models. The cover image shows a root mass in a decaying palmetto rhizhome taken from a scrub-oak forest at Kennedy Space Center, Florida, USA during a 2004–2005 campaign to determine root biomass from ground-penetrating radar. Courtesy of Frank P. Day (Old Dominion University).

Turn the page to read the articles…

Introduction

The origins of this *Virtual Special Issue* lie in a workshop titled Scaling Root Processes: Global Impacts, held in Washington, D.C. on March 7–9, 2012. The workshop was organized in response to the growing recognition of the importance of terrestrial ecosystems in the global carbon cycle and the need to improve model representations of carbon flow within ecosystems by bringing root functions into models.

The workshop brought together over 50 researchers to discuss new research approaches and technologies for improving our fundamental understanding of root processes and their representation in predictive climate models. Many of the articles included in this collection originated from the workshop discussions. Others in the collection have been selected from the *New Phytologist* archive. The journal has a long history of publishing important work on root biology, particularly in relation to global change issues, and this collection serves to further enhance the understanding of root systems and their dynamic interactions with broader ecosystem-level processes.

Read Commentary

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Research

Modeling forest stand dynamics from optimal balances of carbon and nitrogen

Harry T. Valentine, Annikki Mäkelä

Summary

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New Phytologist (2012) **194**: 961 - 971
doi: 10.1111/j.1469-8137.2012.04123.x

Key words: allocation, biomass, carbon (C), growth model, optimization, pipe model, productivity, stand dynamics.

• We formulate a dynamic evolutionary optimization problem to predict the optimal pattern by which carbon (C) and nitrogen (N) are co-allocated to fine-root, leaf, and wood production, with the objective of maximizing height growth rate, year by year, in an even-aged stand.
• Height growth is maximized with respect to two adaptive traits, leaf N concentration and the ratio of fine-root mass to sapwood cross-sectional area. Constraints on the optimization include pipe-model structure, the C cost of N acquisition, and agreement between the C and N balances. The latter is determined by two models of height growth rate, one derived from the C balance and the other from the N balance; agreement is defined by identical growth rates.
• Predicted time-courses of maximized height growth rate accord with general observations. Across an N gradient, higher N availability leads to greater N utilization and net primary productivity, larger trees, and greater stocks of leaf and live wood biomass, with declining gains as a result of saturation effects at high N availability. Fine-root biomass is greatest at intermediate N availability.
• Predicted leaf and fine-root stocks agree with data from coniferous stands across Finland. Optimal C-allocation patterns agree with published observations and model analyses.

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Research

Responses of belowground carbon allocation dynamics to extended shading in mountain grassland

Michael Bahn, Fernando A. Lattanzi, Roland Hasibeder, Birgit Wild, Marianne Koranda, Valentina Danese, Nicolas Brüggemann, Michael Schmitt, Rolf Siegwolf, Andreas Richter

Summary

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New Phytologist (2013) **198**: 116 - 126
doi: 10.1111/nph.12138

Key words: ^{13}C tracer experiment, carbohydrate pools, carbon allocation, microbial phospholipid fatty acid (PLFA), respiration, starch, sugar.

• Carbon (C) allocation strongly influences plant and soil processes. Short-term C allocation dynamics in ecosystems and their responses to environmental changes are still poorly understood.
• Using *in situ* $^{13}CO_2$ pulse labeling, we studied the effects of 1 wk of shading on the transfer of recent photoassimilates between sugars and starch of above- and belowground plant organs and to soil microbial communities of a mountain meadow.
• C allocation to roots and microbial communities was rapid. Shading strongly reduced sucrose and starch concentrations in shoots, but not roots, and affected tracer dynamics in sucrose and starch of shoots, but not roots: recent C was slowly incorporated into root starch irrespective of the shading treatment. Shading reduced leaf respiration more strongly than root respiration. It caused no reduction in the amount of ^{13}C incorporated into fungi and Gram-negative bacteria, but increased its residence time.
• These findings suggest that, under interrupted C supply, belowground C allocation (as reflected by the amount of tracer allocated to root starch, soil microbial communities and belowground respiration) was maintained at the expense of aboveground C status, and that C source strength may affect the turnover of recent plant-derived C in soil microbial communities.

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Research

New insights into carbon allocation by trees from the hypothesis that annual wood production is maximized

Ross E. McMurtrie, Roderick C. Dewar

Summary

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New Phytologist (2013) **199**: 981 - 990
doi: 10.1111/nph.12344

Key words: canopy photosynthesis, gross primary production, leaf area index, maximum wood production, optimization model, root nitrogen uptake, rooting depth, tree carbon allocation.

• Allocation of carbon (C) between tree components (leaves, fine roots and woody structures) is an important determinant of terrestrial C sequestration. Yet, because the mechanisms underlying C allocation are poorly understood, it is a weak link in current earth-system models. We obtain new theoretical insights into C allocation from the hypothesis (*MaxW*) that annual wood production is maximized.
• *MaxW* is implemented using a model of tree C and nitrogen (N) balance with a vertically resolved canopy and root system for stands of Norway spruce (*Picea abies*).
• *MaxW* predicts optimal vertical profiles of leaf N and root biomass, optimal canopy leaf area index and rooting depth, and the associated optimal pattern of C allocation.
• Key insights include a predicted optimal C–N functional balance between leaves at the base of the canopy and the deepest roots, according to which the net C export from basal leaves is just sufficient to grow the basal roots required to meet their N requirement. *MaxW* links the traits of basal leaves and roots to whole-tree C and N uptake, and unifies two previous optimization hypotheses (maximum gross primary production, maximum N uptake) that have been applied independently to canopies and root systems.

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Review

Research Review

Root stress and nitrogen deposition: consequences and research priorities

Erica A. H. Smithwick, David M. Eissenstat, Gary M. Lovett, Richard D. Bowden, Lindsey E. Rustad, Charles T. Driscoll

Summary

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New Phytologist (2013) **197**: 712 - 719
doi: 10.1111/nph.12081

Key words: allocation, aluminum (Al), drought, model, nitrogen deposition, root biogeochemical stress, root lifespan, threshold.

Stress within tree roots may influence whole-tree responses to nutrient deficiencies or toxic ion accumulation, but the mechanisms that govern root responses to the belowground chemical environment are poorly quantified. Currently, root production is modeled using rates of forest production and stoichiometry, but this approach alone may be insufficient to forecast variability in forest responses when physical and chemical stressors alter root lifespan, rooting depth or mycorrhizal colonization directly. Here, we review key research priorities for improving predictions of tree responses to changes in the belowground biogeochemical environment resulting from nitrogen deposition, including: limits of the optimum allocation paradigm, root physiological stress and lifespan, contingency effects that determine threshold responses across broad gradients, coupled water-biogeochemical interactions on roots, mycorrhizal dynamics that mediate root resilience and model frameworks to better simulate root feedbacks to aboveground function. We conclude that models incorporating physiological feedbacks, dynamic responses to coupled stressors, mycorrhizal interactions, and which challenge widely accepted notions of optimum allocation, can elucidate potential thresholds of tree responses to biogeochemical stressors. Emphasis on comparative studies across species and environmental gradients, and which incorporates insights at the cellular and ecosystem level, is critical for forecasting whole-tree responses to altered biogeochemical landscapes.

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Research

Temporal dynamics of fine roots under long-term exposure to elevated CO_2 in the Mojave Desert

Derek L. Sonderegger, Kiona Ogle, R. Dave Evans, Scot Ferguson, Robert S. Nowak

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New Phytologist (2013) **138**: 127 - 138
doi: 10.1111/nph.12128

Key words: *Ambrosia dumosia*, Bayesian, elevated CO_2, FACE (free-air CO_2 enrichment), fine roots, *Larrea tridentata*, Mojave Desert, temporal dynamics.

Summary

- Deserts are considered 'below-ground dominated', yet little is known about the impact of rising CO_2 in combination with natural weather cycles on long-term dynamics of root biomass. This study quantifies the temporal dynamics of fine-root production, loss and standing crop in an intact desert ecosystem exposed to 10 yr of elevated CO_2.
- We used monthly minirhizotron observations from 4 yr (2003–2007) for two dominant shrub species and along community transects at the Nevada Desert free-air CO_2 enrichment Facility. Data were synthesized within a Bayesian framework that included effects of CO_2 concentration, cover type, phenological period, antecedent soil water and biological inertia (i.e. the influence of prior root production and loss).
- Elevated CO_2 treatment interacted with antecedent soil moisture and had significantly greater effects on fine-root dynamics during certain phenological periods. With respect to biological inertia, plants under elevated CO_2 tended to initiate fine-root growth sooner and sustain growth longer, with the net effect of increasing the magnitude of production and mortality cycles.
- Elevated CO_2 interacts with past environmental (e.g. antecedent soil water) and biological (e.g. biological inertia) factors to affect fine-root dynamics, and such interactions are expected to be important for predicting future soil carbon pools.

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Research

Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits?

Grégoire T. Freschet, Johannes H. C. Cornelissen, Richard S. P. van Logtestijn, Rien Aerts

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New Phytologist (2010) **186**: 879 - 889
doi: 10.1111/j.1469-8137.2010.03228.x

Key words: leaching resistance, nitrogen, nutrient resorption, organ senescence, phosphorus, plant economics, root, shoot.

Summary

• Nutrient resorption and leaching resistance, through their roles in reducing nutrient losses, are important determinants of plant nutrient economy. However, the contributions of fine-stem and fine-root resorption, as well as leaf leaching resistance, have largely been overlooked.

• We quantified the relative contributions of these processes to nutrient depletion of these organs during their senescence using 40 subarctic vascular species from aquatic, riparian and terrestrial environments. We hypothesized that interspecific variation in organ nutrient resorption and leaf leaching would be linked to the species' nutrient acquisitive-conservative strategies, as quantified for a set of common-organ nutrient/carbon economics traits.

• The subarctic flora generally had both high resistance to leaching and high internal nutrient recycling. Average nutrient resorption efficiencies were substantial for leaves (nitrogen (N), 66 ± 3% SE; phosphorus (P), 63 ± 4%), fine stems (N, 48 ± 4%; P, 56 ± 4%) and fine roots (N, 27 ± 7%; P, 57 ± 6%). The link between nutrient resorption and other nutrient/carbon economics traits was very weak across species, for all three organs.

• These results emphasize the potential importance of resorption processes for the plant nutrient budget. They also highlight the idiosyncrasies of the relationship between resorption processes and plant economics, which is potentially influenced by several plant physiological and structural adaptations to environmental factors other than nutrient stress.

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Review

Research Review

Ecosystem-level controls on root-rhizosphere respiration

Francesca Hopkins, Miquel A. Gonzalez-Meler, Charles E. Flower, Douglas J. Lynch, Claudia Czimczik, Jianwu Tang, Jens-Arne Subke

Summary

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New Phytologist (2013) **199**: 339 - 351
doi: 10.1111/nph.12271

Key words: autotrophic, global change, gross primary productivity (GPP), heterotrophic, nitrogen (N), rhizosphere, root respiration, soil respiration.

Recent advances in the partitioning of autotrophic from heterotrophic respiration processes in soils in conjunction with new high temporal resolution soil respiration data sets offer insights into biotic and environmental controls of respiration. Besides temperature, many emerging controlling factors have not yet been incorporated into ecosystem-scale models. We synthesize recent research that has partitioned soil respiration into its process components to evaluate effects of nitrogen, temperature and photosynthesis on autotrophic flux from soils at the ecosystem level. Despite the widely used temperature dependence of root respiration, gross primary productivity (GPP) can explain most patterns of ecosystem root respiration (and to some extent heterotrophic respiration) at within-season time-scales. Specifically, heterotrophic respiration is influenced by a seasonally variable supply of recent photosynthetic products in the rhizosphere. The contribution of stored root carbon (C) to root respiratory fluxes also varied seasonally, partially decoupling the proportion of photosynthetic C driving root respiration. In order to reflect recent insights, new hierarchical models, which incorporate root respiration as a primary function of GPP and which respond to environmental variables by modifying C allocation belowground, are needed for better prediction of future ecosystem C sequestration.

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Research

Transport of root-respired CO_2 via the transpiration stream affects aboveground carbon assimilation and CO_2 efflux in trees

Jasper Bloemen, Mary Anne McGuire, Doug P. Aubrey, Robert O. Teskey, Kathy Steppe

Summary

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New Phytologist (2013) **187**: 555 - 565
doi: 10.1111/j.1469-8137.2012.04366.x

Key words: carbon allocation, respiration, roots, soil CO_2 efflux, stable isotope, xylem transport.

- Upward transport of CO_2 via the transpiration stream from belowground to aboveground tissues occurs in tree stems. Despite potentially important implications for our understanding of plant physiology, the fate of internally transported CO_2 derived from autotrophic respiratory processes remains unclear.
- We infused a $^{13}CO_2$-labeled aqueous solution into the base of 7-yr-old field-grown eastern cottonwood (*Populus deltoides*) trees to investigate the effect of xylem-transported CO_2 derived from the root system on aboveground carbon assimilation and CO_2 efflux.
- The ^{13}C label was transported internally and detected throughout the tree. Up to 17% of the infused label was assimilated, while the remainder diffused to the atmosphere via stem and branch efflux. The largest amount of assimilated ^{13}C was found in branch woody tissues, while only a small quantity was assimilated in the foliage. Petioles were more highly enriched in ^{13}C than other leaf tissues.
- Our results confirm a recycling pathway for respired CO_2 and indicate that internal transport of CO_2 from the root system may confound the interpretation of efflux-based estimates of woody tissue respiration and patterns of carbohydrate allocation.

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Ephemeral root modules in *Fraxinus mandshurica*

Mengxue Xia, Dali Guo, Kurt S. Pregitzer

Summary

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New Phytologist (2010) **188**: 1065 - 1074
doi: 10.1111/j.1469-8137.2010.03423.x

Key words: branch order, ephemeral roots, fine roots, *Fraxinus mandshurica*, nitrogen concentrations, plant modules, respiration, root turnover.

• Historically, ephemeral roots have been equated with 'fine roots' (i.e. all roots of less than an arbitrary diameter, such as 2 mm), but evidence shows that 'fine roots' in woody species are complex branching systems with both rapid-cycling and slow-cycling components. A precise definition of ephemeral roots is therefore needed.

• Using a branch-order classification, a rhizotron method and sequential sampling of a root cohort, we tested the hypothesis that ephemeral root modules exist within the branching *Fraxinus mandshurica* (Manchurian ash) root system as distal nonwoody lateral branches, which show anatomical, nutritional and physiological patterns distinct from their woody mother roots.

• Our results showed that in *F. mandshurica*, distal nonwoody root branch orders die rapidly as intact lateral branches (or modules). These nonwoody branch orders exhibited highly synchronous changes in tissue nitrogen concentrations and respiration, dominated root turnover, nutrient flux and root respiration, and never underwent secondary development.

• The ephemeral root modules proposed here may provide a functional basis for differentiating and sampling short-lived absorptive roots in woody plants, and represent a conceptual leap over the traditional coarse–fine root dichotomies based on arbitrary size classes.

New Phytologist

Research

Allocation of carbon to fine root compounds and their residence times in a boreal forest depend on root size class and season

Sonja G. Keel, Catherine D. Campbell, Mona N. Högberg, Andreas Richter, Birgit Wild, Xuhui Zhou, Vaughan Hurry, Sune Linder, Torgny Näsholm, Peter Högberg

Summary

- Fine roots play a key role in the forest carbon balance, but their carbon dynamics remain largely unknown.
- We pulse labelled 50 m² patches of young boreal forest by exposure to $^{13}CO_2$ in early and late summer. Labelled photosynthates were traced into carbon compounds of < 1 and 1–3 mm diameter roots (fine roots), and into bulk tissue of these and first-order roots (root tips).
- Root tips were the most strongly labelled size class. Carbon allocation to all size classes was higher in late than in early summer; mean residence times (MRTs) in starch increased from 4 to 11 months. In structural compounds, MRTs were 0.8 yr in tips and 1.8 yr in fine roots. The MRT of carbon in sugars was in the range of days.
- Functional differences within the fine root population were indicated by carbon allocation patterns and residence times. Pronounced allocation of recent carbon and higher turnover rates in tips are associated with their role in nutrient and water acquisition. In fine roots, longer MRTs but high allocation to sugars and starch reflect their role in structural support and storage. Accounting for heterogeneity in carbon residence times will improve and most probably reduce the estimates of fine root production.

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New Phytologist (2012) **194**: 972 - 981
doi: 10.1111/j.1469-8137.2012.04120.x

Key words: carbon cycling, carbon isotope, carbon reserves, fine roots, forest, residence time, starch, sugars.

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Research

Fine-root mortality rates in a temperate forest: estimates using radiocarbon data and numerical modeling

W. J. Riley, J. B. Gaudinski, M. S. Torn, J. D. Joslin, P. J. Hanson

Summary

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New Phytologist (2009) **184**: 387 - 398
doi: 10.1111/j.1469-8137.2009.02980.x

Key words: carbon cycling, carbon isotope, fine-root turnover time, MonteCarlo simulations, numerical model, radiocarbon, root model parameterization, roots.

• We used an inadvertent whole-ecosystem ^{14}C label at a temperate forest in Oak Ridge, Tennessee, USA to develop a model (*Radix*1.0) of fine-root dynamics. *Radix* simulates two live-root pools, two dead-root pools, non-normally distributed root mortality turnover times, a stored carbon (C) pool, and seasonal growth and respiration patterns.
• We applied *Radix* to analyze measurements from two root size classes (< 0.5 and 0.5–2.0 mm diameter) and three soil-depth increments (O horizon, 0–15 cm and 30–60 cm).
• Predicted live-root turnover times were < 1 yr and ~10 yr for short- and long- lived pools, respectively. Dead-root pools had decomposition turnover times of ~2 yr and ~10 yr. Realistic characterization of C flows through fine roots requires a model with two live fine-root populations, two dead fine-root pools, and root respiration. These are the first fine-root turnover time estimates that take into account respiration, storage, seasonal growth patterns, and non-normal turnover time distributions.
• The presence of a root population with decadal turnover times implies a lower amount of belowground net primary production used to grow fine-root tissue than is currently predicted by models with a single annual turnover pool.

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Research

Stored carbon partly fuels fine-root respiration but is not used for production of new fine roots

Douglas J. Lynch, Roser Matamala, Colleen M. Iversen, Richard J. Norby, Miquel A. Gonzalez-Meler

Summary

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New Phytologist (2013) **199**: 420 - 430
doi: 10.1111/nph.12290

Key words: ^{13}C, fine roots, free-air CO_2 enrichment (FACE), post-carboxylation fractionation, root respiration, root turnover, stored carbon (C), *Liquidambar styraciflua*.

• The relative use of new photosynthate compared to stored carbon (C) for the production and maintenance of fine roots, and the rate of C turnover in heterogeneous fine-root populations, are poorly understood.
• We followed the relaxation of a ^{13}C tracer in fine roots in a *Liquidambar styraciflua* plantation at the conclusion of a free-air CO_2 enrichment experiment. Goals included quantifying the relative fractions of new photosynthate vs stored C used in root growth and root respiration, as well as the turnover rate of fine-root C fixed during [CO_2] fumigation.
• New fine-root growth was largely from recent photosynthate, while nearly one-quarter of respired C was from a storage pool. Changes in the isotopic composition of the fine-root population over two full growing seasons indicated heterogeneous C pools; < 10% of root C had a residence time < 3 months, while a majority of root C had a residence time > 2 yr.
• Compared to a one-pool model, a two-pool model for C turnover in fine roots (with 5 and 0.37 yr^{-1} turnover times) doubles the fine-root contribution to forest NPP (9–13%) and supports the 50% root-to-soil transfer rate often used in models.

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Research

Topographic and soil influences on root productivity of three bioenergy cropping systems

Todd A. Ontl, Kirsten S. Hofmockel, Cynthia A. Cambardella, Lisa A. Schulte, Randall K. Kolka

Summary

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New Phytologist (2013) **199**: 727 - 737
doi: 10.1111/nph.12302

Key words: bioenergy, carbon allocation, carbon cycle, ecosystem modeling, root production, scaling, soil variability.

• Successful modeling of the carbon (C) cycle requires empirical data regarding species-specific root responses to edaphic characteristics. We address this need by quantifying annual root production of three bioenergy systems (continuous corn, triticale/sorghum, switchgrass) in response to variation in soil properties across a toposequence within a Midwestern agroecosystem.
• Using ingrowth cores to measure annual root production, we tested for the effects of topography and 11 soil characteristics on root productivity.
• Root production significantly differed among cropping systems. Switchgrass root productivity was lowest on the floodplain position, but root productivity of annual crops was not influenced by topography or soil properties. Greater switchgrass root production was associated with high percent sand, which explained 45% of the variation. Percent sand was correlated negatively with soil C and nitrogen and positively with bulk density, indicating this variable is a proxy for multiple important soil properties.
• Our results suggest that easily measured soil parameters can be used to improve model predictions of root productivity in bioenergy switchgrass, but the edaphic factors we measured were not useful for predicting root productivity in annual crops. These results can improve C cycling modeling efforts by revealing the influence of cropping system and soil properties on root productivity.

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Research

Predicting fine root lifespan from plant functional traits in temperate trees

M. Luke McCormack, Thomas S. Adams, Erica A. H. Smithwick, David M. Eissenstat

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New Phytologist (2012) **195**: 823 - 831
doi: 10.1111/j.1469-8137.2012.04198.x

Key words: ecosystem modeling, functional traits, minirhizotron, root turnover, scaling, temperate forest.

Summary

• Although linkages of leaf and whole-plant traits to leaf lifespan have been rigorously investigated, there is a limited understanding of similar linkages of whole-plant and fine root traits to root lifespan. In comparisons across species, do suites of traits found in leaves also exist for roots, and can these traits be used to predict root lifespan?

• We observed the fine root lifespan of 12 temperate tree species using minirhizotrons in a common garden and compared their median lifespans with fine-root and whole-plant traits. We then determined which set of combined traits would be most useful in predicting patterns of root lifespan.

• Median root lifespan ranged widely among species (95–336 d). Root diameter, calcium content, and tree wood density were positively related to root lifespan, whereas specific root length, nitrogen (N) : carbon (C) ratio, and plant growth rate were negatively related to root lifespan. Root diameter and plant growth rate, together (R^2 = 0.62) or in combination with root N : C ratio (R^2 = 0.76), were useful predictors of root lifespan across the 12 species.

• Our results highlight linkages between fine root lifespan in temperate trees and plant functional traits that may reduce uncertainty in predictions of root lifespan or turnover across species at broader spatial scales.

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New Phytologist

Review

Tansley Review
Water release through plant roots: new insights into its consequences at the plant and ecosystem level

Iván Prieto, Cristina Armas, Francisco I. Pugnaire

Summary

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New Phytologist (2012) **193**: 830 - 841
doi: 10.1111/j.1469-8137.2011.04039.x

Key words: biogeochemical cycles, hydraulic lift, hydraulic redistribution (HR), hydrology, mechanisms, nutrient cycling, plant interactions, root properties.

Hydraulic redistribution (HR) is the passive movement of water between different soil parts via plant root systems, driven by water potential gradients in the soil–plant interface. New data suggest that HR is a heterogeneous and patchy process. In this review we examine the main biophysical and environmental factors controlling HR and its main implications at the plant, community and ecosystem levels. Experimental evidence and the use of novel modelling approaches suggest that HR may have important implications at the community scale, affecting net primary productivity as well as water and vegetation dynamics. Globally, HR may influence hydrological and biogeochemical cycles and, ultimately, climate.

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Review

Tansley Review

The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies

Rebecca B. Neumann, Zoe G. Cardon

Summary

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New Phytologist (2012) **194**: 337 - 352
doi: 10.1111/j.1469-8137.2012.04088.x

Key words: ecosystem, hydraulic lift, hydraulic redistribution (HR), hydrology, plant roots, review, soil.

Hydraulic redistribution (HR) – the movement of water from moist to dry soil through plant roots – occurs worldwide within a range of different ecosystems and plant species. The proposed ecological and hydrologic impacts of HR include increasing dry-season transpiration and photosynthetic rates, prolonging the life span of fine roots and maintaining root–soil contact in dry soils, and moving rainwater down into deeper soil layers where it does not evaporate. In this review, we compile estimates of the magnitude of HR from ecosystems around the world, using representative empirical and modeling studies from which we could extract amounts of water redistributed by plant root systems. The reported average magnitude of HR varies by nearly two orders of magnitude across ecosystems, from 0.04 to 1.3 mm H_2O d^{-1} in the empirical literature, and from 0.1 to 3.23 mm H_2O d^{-1} in the modeling literature. Using these synthesized data, along with other published studies, we examine this variation in the magnitude of upward and downward HR, considering effects of plant, soil and ecosystem characteristics, as well as effects of methodological details (in both empirical and modeling studies) on estimates of HR. We take both ecological and hydrologic perspectives.

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New Phytologist

Research

Three-dimensional visualization and quantification of water content in the rhizosphere

Ahmad B. Moradi, Andrea Carminati, Doris Vetterlein, Peter Vontobel, Eberhard Lehmann, Ulrich Weller, Jan W. Hopmans, Hans-Jörg Vogel, Sascha E. Oswald

Summary

• Despite the importance of rhizosphere properties for water flow from soil to roots, there is limited quantitative information on the distribution of water in the rhizosphere of plants.

• Here, we used neutron tomography to quantify and visualize the water content in the rhizosphere of the plant species chickpea (*Cicer arietinum*), white lupin (*Lupinus albus*), and maize (*Zea mays*) 12 d after planting.

• We clearly observed increasing soil water contents (Θ) towards the root surface for all three plant species, as opposed to the usual assumption of decreasing water content. This was true for tap roots and lateral roots of both upper and lower parts of the root system. Furthermore, water gradients around the lower part of the roots were smaller and extended further into bulk soil compared with the upper part, where the gradients in water content were steeper.

• Incorporating the hydraulic conductivity and water retention parameters of the rhizosphere into our model, we could simulate the gradual changes of Θ towards the root surface, in agreement with the observations. The modelling result suggests that roots in their rhizosphere may modify the hydraulic properties of soil in a way that improves uptake under dry conditions.

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doi: 10.1111/j.1469-8137.2011.03826.x

Key words: extent of rhizosphere, modelling, neutron tomography, rhizosphere hydraulic properties, root water uptake, soil moisture profile, water distribution.

Read Full Article

New Phytologist

Review

Tansley Review

Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance

Yakov Kuzyakov, Xingliang Xu

Summary

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New Phytologist (2013) **198**: 656 - 659
doi: 10.1111/nph.12235

Key words: carbon (C) and nitrogen (N) turnover, competition for nitrogen (N) and phosphorus (P), mutualism, niche differentiation, nutrient acquisition, plant–microbe interactions, priming effect, rhizosphere ecology.

Read Full Article

Demand of all living organisms on the same nutrients forms the basis for interspecific competition between plants and microorganisms in soils. This competition is especially strong in the rhizosphere. To evaluate competitive and mutualistic interactions between plants and microorganisms and to analyse ecological consequences of these interactions, we analysed 424 data pairs from 41 ^{15}N-labelling studies that investigated ^{15}N redistribution between roots and microorganisms. Calculated Michaelis–Menten kinetics based on K_m (Michaelis constant) and V_{max} (maximum uptake capacity) values from 77 studies on the uptake of nitrate, ammonia, and amino acids by roots and microorganisms clearly showed that, shortly after nitrogen (N) mobilization from soil organic matter and litter, microorganisms take up most N. Lower K_m values of microorganisms suggest that they are especially efficient at low N concentrations, but can also acquire more N at higher N concentrations (V_{max}) compared with roots. Because of the unidirectional flow of nutrients from soil to roots, plants are the winners for N acquisition in the long run. Therefore, despite strong competition between roots and microorganisms for N, a temporal niche differentiation reflecting their generation times leads to mutualistic relationships in the rhizosphere. This temporal niche differentiation is highly relevant ecologically because it: protects ecosystems from N losses by leaching during periods of slow or no root uptake; continuously provides roots with available N according to plant demand; and contributes to the evolutionary development of mutualistic interactions between roots and microorganisms.

New Phytologist

Review

Research Review

The mycorrhizal-associated nutrient economy: a new framework for predicting carbon – nutrient couplings in temperate forests

Richard P. Phillips, Edward Brzostek, Meghan G. Midgley

Summary

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New Phytologist (2013) **199**: 41 - 51
doi: 10.1111/nph.12221

Key words: arbuscular mycorrhizal (AM) fungi, ectomycorrhizal (ECM) fungi, mycorrhizal associations, plant–microbial feedbacks, rhizosphere.

Understanding the context dependence of ecosystem responses to global changes requires the development of new conceptual frameworks. Here we propose a framework for considering how tree species and their mycorrhizal associates differentially couple carbon (C) and nutrient cycles in temperate forests. Given that tree species predominantly associate with a single type of mycorrhizal fungi (arbuscular mycorrhizal (AM) fungi or ectomycorrhizal (ECM) fungi), and that the two types of fungi differ in their modes of nutrient acquisition, we hypothesize that the abundance of AM and ECM trees in a plot, stand, or region may provide an integrated index of biogeochemical transformations relevant to C cycling and nutrient retention. First, we describe how forest plots dominated by AM tree species have nutrient economies that differ in their C–nutrient couplings from those in plots dominated by ECM trees. Secondly, we demonstrate how the relative abundance of AM and ECM trees can be used to estimate nutrient dynamics across the landscape. Finally, we describe how our framework can be used to generate testable hypotheses about forest responses to global change factors, and how these dynamics can be used to develop better representations of plant–soil feedbacks and nutrient constraints on productivity in ecosystem and earth system models.

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New Phytologist

Review

Tansley Review

Synthesis and modeling perspectives of rhizosphere priming

Weixin Cheng, William J. Parton, Miquel A. Gonzalez-Meler, Richard Phillips, Shinichi Asao, Gordon G. McNickle, Edward Brzostek, Julie D. Jastrow

Summary

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New Phytologist (2013)
doi: 10.1111/nph.12440

Key words: decomposition, elevated CO_2, PhotoCent model, plant–microbe interactions, roots, soil organic matter (SOM).

The rhizosphere priming effect (RPE) is a mechanism by which plants interact with soil functions. The large impact of the RPE on soil organic matter decomposition rates (from 50% reduction to 380% increase) warrants similar attention to that being paid to climatic controls on ecosystem functions. Furthermore, global increases in atmospheric CO_2 concentration and surface temperature can significantly alter the RPE. Our analysis using a game theoretic model suggests that the RPE may have resulted from an evolutionarily stable mutualistic association between plants and rhizosphere microbes. Through model simulations based on microbial physiology, we demonstrate that a shift in microbial metabolic response to different substrate inputs from plants is a plausible mechanism leading to positive or negative RPEs. In a case study of the Duke Free-Air CO_2 Enrichment experiment, performance of the PhotoCent model was significantly improved by including an RPE-induced 40% increase in soil organic matter decomposition rate for the elevated CO_2 treatment – demonstrating the value of incorporating the RPE into future ecosystem models. Overall, the RPE is emerging as a crucial mechanism in terrestrial ecosystems, which awaits substantial research and model development.

New Phytologist

Review

Minireview

Digging deeper: fine root responses to rising atmospheric CO_2 in forested ecosystems

Colleen M. Iversen

Summary

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New Phytologist (2010) **186**: 346 - 357
doi: 10.1111/j.1469-8137.2009.03122.x

Key words: carbon storage, depth distribution, ecosystem model, elevated [CO_2], forests, fine roots, nutrient cycling, turnover.

Experimental evidence from a diverse set of forested ecosystems indicates that CO_2 enrichment may lead to deeper rooting distributions. While the causes of greater root production at deeper soil depths under elevated CO_2 concentration ([CO_2]) require further investigation, altered rooting distributions are expected to affect important ecosystem processes. The depth at which fine roots are produced may influence root chemistry, physiological function, and mycorrhizal infection, leading to altered nitrogen (N) uptake rates and slower turnover. Also, soil processes such as microbial decomposition are slowed at depth in the soil, potentially affecting the rate at which root detritus becomes incorporated into soil organic matter. Deeper rooting distributions under elevated [CO_2] provide exciting opportunities to use novel sensors and chemical analyses throughout the soil profile to track the effects of root proliferation on carbon (C) and N cycling. Models do not currently incorporate information on root turnover and C and N cycling at depth in the soil, and modification is necessary to accurately represent processes associated with altered rooting depth distributions. Progress in understanding and modeling the interface between deeper rooting distributions under elevated [CO_2] and soil C and N cycling will be critical in projecting the sustainability of forest responses to rising atmospheric [CO_2].

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New Phytologist

Research

In situ high-frequency observations of mycorrhizas

Michael F. Allen, Kuni Kitajima

Summary

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New Phytologist (2013) **200**: 222 - 228
doi: 10.1111/nph.12363

Key words: automated minirhizotron, carbon scaling, conifer forest, ectomycorrhiza, hyphae, production, soil sensor network, turnover.

• Understanding the temporal variation of soil and root dynamics is a major step towards determining net carbon in ecosystems. We describe the installation and structure of an *in situ* soil observatory and sensing network consisting of an automated minirhizotron with associated soil and atmospheric sensors.
• Ectomycorrhizal hyphae were digitized daily during 2011 in a Mediterranean climate, high elevation coniferous forest. Hyphal length was high, but stable during winter in moist and cold soil. As soil began to warm and dry, simultaneous mortality and production indicating turnover followed precipitation events. Mortality continued through the dry season, although some hyphae persisted through the extremes. With autumn monsoons, rapid hyphal re-growth occurred following each event.
• Relative hyphal length is dependent upon soil temperature and moisture. Soil respiration is related to the daily change in hyphal production, but not hyphal mortality.
• Continuous sensor and observation systems can provide more accurate assessments of soil carbon dynamics.

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New Phytologist

Review

Tansley Review

Through the eye of a needle: a review of isotope approaches to quantify microbial processes mediating soil carbon balance

Eric Paterson, Andrew J. Midwood, Peter Millard

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New Phytologist (2009) **184**: 19 - 33
doi: 10.1111/j.1469-8137.2009.03001.x

Key words: isotopic labelling, natural abundance isotopic methods, respiration partitioning, rhizodeposition, soil carbon balance, soil microbial communities, soil organic matter, soil respiration.

Summary

For soils in carbon balance, losses of soil carbon from biological activity are balanced by organic inputs from vegetation. Perturbations, such as climate or land use change, have the potential to disrupt this balance and alter soil–atmosphere carbon exchanges. As the quantification of soil organic matter stocks is an insensitive means of detecting changes, certainly over short timescales, there is a need to apply methods that facilitate a quantitative understanding of the biological processes underlying soil carbon balance. We outline the processes by which plant carbon enters the soil and critically evaluate isotopic methods to quantify them. Then, we consider the balancing CO_2 flux from soil and detail the importance of partitioning the sources of this flux into those from recent plant assimilate and those from native soil organic matter. Finally, we consider the interactions between the inputs of carbon to soil and the losses from soil mediated by biological activity. We emphasize the key functional role of the microbiota in the concurrent processing of carbon from recent plant inputs and native soil organic matter. We conclude that quantitative isotope labelling and partitioning methods, coupled to those for the quantification of microbial community substrate use, offer the potential to resolve the functioning of the microbial control point of soil carbon balance in unprecedented detail.

Read Full Article

New Phytologist

Research

A dual porosity model of nutrient uptake by root hairs

K. C. Zygalakis, G.J.D. Kirk, D. L. Jones, M. Wissuwa, T. Roose

Summary

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New Phytologist (2011) **192**: 676 - 688
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Key words: mathematical model, nutrient uptake, phosphate, rhizosphere, root hairs.

• The importance of root hairs in the uptake of sparingly soluble nutrients is understood qualitatively, but not quantitatively, and this limits efforts to breed plants tolerant of nutrient-deficient soils.
• Here, we develop a mathematical model of nutrient uptake by root hairs allowing for hair geometry and the details of nutrient transport through soil, including diffusion within and between soil particles. We give illustrative results for phosphate uptake.
• Compared with conventional 'single porosity' models, this 'dual porosity' model predicts greater root uptake because more nutrient is available by slow release from within soil particles. Also the effect of soil moisture is less important with the dual porosity model because the effective volume available for diffusion in the soil is larger, and the predicted effects of hair length and density are different.
• Consistent with experimental observations, with the dual porosity model, increases in hair length give greater increases in uptake than increases in hair density per unit main root length. The effect of hair density is less in dry soil because the minimum concentration in solution for net influx is reached more rapidly. The effect of hair length is much less sensitive to soil moisture.

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